

## ECOLOGY OF THE SPIDERS OF A DESERT COMMUNITY<sup>1</sup>

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### INTRODUCTION

There has been only a moderate amount of work on the synecology of spiders. As expected, the data that are available show that this order of arthropods conforms to ecological principles well demonstrated for other groups. For example: (1) Biotic communities have distinct spider faunas, characterized by the frequency and density of the component species, as very nicely shown by Barnes (1953) for *Spartina* tidal marsh and Barnes and Barnes (1955) for the *Andropogon* seral stage in oldfield succession. Holm (1950) found characteristic spiders according to biotopes in Swedish Lapland. (2) There is a distinct change in spider fauna with succession (Gibson 1947, Lowrie 1948, Dowdy 1950, Barnes 1953, Barnes and Barnes 1954). (3) Different spider populations within a community show both spatial stratification (Elliott 1930, Lowrie 1948, Dowdy 1950, 1951, Kuenzler 1958) and temporal stratification, the latter on a diel rhythm (Muma and Muma 1949) and seasonal pattern (Gibson 1947, Fichter 1954, Barnes and Barnes 1955). (4) The interaction of the physical environmental factors of temperature and humidity with the different temperature preferences, upper limits of temperature tolerance, and rates of desiccation of different spiders, is very important in determining geographic, microhabitat and temporal distributions of spider populations (Lowrie 1942, Holm 1950, Nørgaard 1951, Nemenz 1954). (5) Biotic factors also influence distribution, as stressed by Tretzel (1955).

The present report is a part of a more comprehensive study of the ecology of a desert shrub community dominated by creosote bush (*Larrea divaricata*), the widespread dominant of the hot deserts of southwestern North America. The spider populations deserve special attention, since only one other work has dealt with

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the ecology of desert inhabiting spiders, that of Fautin (1946), treating the ecology of communities in the northern cool deserts of North America, dominated by *Artemesia* over wide areas.

#### STUDY AREA AND METHODS

The present study was conducted on a fenced 22-acre plot located in the San Simone Valley, 5 miles north of Portal, Cochise County, Arizona (T17S-R31E-S3). The plot, part of the Z-T Ranch, was generously made available for unlimited use by the owner, Mr. Herman Kollmar.

The desert shrub vegetation of this general region probably is a grazing disclimax in an area formerly desert plains grassland. In the study area, total shrub cover was 20.7 per cent, which was almost entirely due to three species: *Larrea divaricata* (creosote bush) 17.35 per cent cover, *Flourensia cernua* (tarbush) 1.12 per cent, and *Parthenium incanum* (mariola) 1.59 per cent. Herb cover was very sparse and only temporary, reaching 1.48 per cent in August, which is about its maximum development. The most abundant herb was a grass, *Muhlenbergia porteri* (0.47 per cent cover), which grew principally under the shrubs. The next three herbs, in amount of coverage, were *Bahia absinthifolia* (composite), 0.24 per cent, *Tridens pulchellus* (grass), 0.21 per cent and *Hoffmanseggia densiflora* (legume), 0.17 per cent.

No long term weather data are available for the immediate vicinity of the study plot, and because of irregularities introduced by the proximity of the Chiricahua Mountains, data for the nearest weather stations may not be very applicable. The San Simone weather station, about 25 miles north of the study plot records an average annual rainfall of 7.9 inches, more than 60 per cent of this coming in the period July through October. April through June is practically without rain. The Portal weather station, 5 miles to the south, but located in the mouth of a canyon, records an annual rainfall of 18.9 inches, with the same seasonal distribution as San Simone. San Simone records show mean monthly temperatures ranging from a low of 7.0° C. in January to 28.6° C. in July.

The arthropods of the shrub stratum in the study area were collected by means of sets of 48-sweeps taken with an insect net 30 cm. in diameter. Usually each individual sweep was from a different bush. Sweeps were taken at about monthly intervals,



from September 1958 through August 1959. Usually 4 sets of sweeps were taken from creosote bush and 2 sets each from tarbush and mariola. For each set of sweeps, individual arthropods were sorted and counted according to species, and fresh weights were measured for species lumped together into certain taxonomic groups.

Individual spiders were examined under a stereoscopic microscope, and the total length of each was measured. Total length was the most easily measured dimension, and in several large samples it proved as reliable in size ranking of individuals as cephalothorax width. Size frequency distributions were plotted using a 0.04 mm. size group basis. The total collections involved 73 sets of 48-sweeps containing 817 individual spiders.

A standard set of 48-sweeps is generally considered to give a sample of arthropods equivalent to that in the vegetation over one square meter of surface. This calibration has been established in the herb stratum in deciduous forest (Shelford 1951) and the same quantitative relationship has been assumed to hold for shrub sweeps (as by Fautin 1946, and others). However the precision with which shrub sweeps can be made is much less than that for herb sweeps. The efficiency of sweeping also varies with the sizes of the individual shrubs (as it limits the length of sweep), and the flexibility of the leaved branches. The three shrubs in the present study varied considerably in these respects. Creosote bush, the largest and most flexible of the shrubs, was the most efficiently swept, while tarbush, the most rigid, and mariola, the smallest, were less effectively swept. In the present methods, two short sweeps from small shrubs were counted as one sweep.

Obviously the most reliable use of 48-sweep data is as density indices in particular shrubs. However, for means of comparison and incorporation with other quantitative data, absolute densities of spiders were calculated in the present study, assuming that 48 sweeps = 1 M<sup>2</sup>.

Due to lack of time and of quantitative methods adequate for a desert situation, the arthropods of the ground and subterranean strata, and of the herbs, were not sampled. It is felt that the spiders of these strata are quantitatively much less important than those of the shrubs. Fautin (1946) studied the ground stratum in sagebrush desert, but does not mention any spider as being a significant part of the arthropod communities. In 17

TABLE 1. AVERAGE NUMBER OF INDIVIDUALS PER 48-SWEEPS, ACCORDING TO SPECIES OF SPIDER, KIND OF SHRUB, AND COLLECTION DATE. L = creosote bush, *Larrea divaricata*, F = tarbush, *Flourensia cernua*, P = mariola, *Parthenium incanum*. Number in parentheses is number of sets of 48-sweeps involved in average.

	20 Sept.		20 Oct. 1958			2 Dec. 1958			4 Feb. 1959		
	L (6)	F (1)	L (4)	F (3)	P (1)	L (4)	F (3)	P (1)	L (4)	F (2)	P (2)
<b>THOMISIDAE</b>											
<i>Misumenops</i> spp. juv.	9.3	7.0	8.5	5.7	4.0	3.0	3.0	2.0			
<i>M. dubius</i> (Keyserling)	0.2 ♂		0.2 ♂								
<i>M. coloradensis</i> Gertsch				0.3 ♂							
<i>Philodromus</i> <i>infuscatus</i> Keyserling	0.2 ♂			0.3j	2.0j						
<i>Tmarus angulatus</i> (Walckenaer)	0.8j		0.8j	1.3j		1.0j	1.3j			2.0j	
<i>Ebo albocaudatus</i> n.sp.* and <i>E. parabolis</i> n.sp.		0.3j			2.0j			1.0j			
<b>SALTICIDAE</b>											
<i>Sassacus papenhoei</i> Peckham	3.3j				1.0j	0.8j	0.3j		0.3j	0.5j	
<i>Phidippus</i> sp.	1.2j		0.3j				0.3j				
<i>Habronattus</i> sp.	1.0j										
unidentified	0.2j		0.3j	1.0j	1.0j		0.3j		0.3j		
<b>ARGIOPIDAE</b>											
<i>Metepeira arizonica</i> Chamberlin & Ivie	0.5j		0.3j	1.7j		0.3j	0.7j	1.0 ♂	0.3j		2.0j
<i>Eustala</i> sp.	0.2j					0.3 ♂				0.5j	
<i>Hamataliva grisea</i> Keyserling			2.0j			0.8j					
<b>DICTYNIDAE</b>											
<i>Dictyna peon</i> Chamberlin & Gertsch					1.0j			1.0 ♂		0.5j	
All species											
Total individuals	16.7	7.0	12.3	11.0	12.0	6.3	6.7	5.0	1.3	3.0	2.0
Total biomass, mg.	43.6	35.5	44.5	46.2	40.9	11.8	14.3	12.5	5.7	7.4	2.5

\* descriptions of these new species are in manuscript, Dr. Robert Schick.

In addition to the above species, the following spiders were taken only once in sweep collections: DIGUETIDAE, *Diguetia canities* (McCook), 1 individual on *Larrea* 27 Aug. 1959; OXYOPIDAE, *Oxyopes* sp., 1 individual on *Parthenium* 2 Dec. 1958; ARGIOPIDAE, *Peucetia viridans* Hentz, 1 individual on *Larrea* 2 Dec. 1958; SALTICIDAE, *Pseudicius piraticus* Peckham, 1 ♂ on *Larrea* 23 June 1959; MICRYPHANTIDAE, *Grammonota sclerata* Chamberlin & Gertsch, 2 individuals on *Parthenium* 4 April 1959; LINYPHIIDAE, *Meioneta* sp., 1 individual on *Flourensia* 2 Dec. 1958; CLUBIONIDAE, *Chiracanthium inclusum* Hentz, 1 individual on *Flourensia* 16 May 1959. *Xysticus aprilius* Bryant, THOMISIDAE, was taken in *Gutierrezia* 25 July 1959; this is the only time this shrub was swept.



stomachs of lizards examined in the present study, there was only one spider present in more than 1300 food items; 3 scorpions and 1 solpugid were present in the same stomach contents. If these

4 April 1959			16 May 1959			23 June 1959			25 July 1959			27 Aug. 1959		
L (4)	F (2)	P (2)	L (4)	F (2)	P (2)	L (4)	F (2)	P (2)	L (4)	F (2)	P (2)	L (6)	F (2)	P (2)
11.3	4.0	2.5	9.5	15.5	2.0	7.5	1.5	0.5	5.1	2.0		2.8		4.0
0.3 ♂	1.5 ♂		0.5 ♂ 0.8 ♀			0.3 ♂ 0.5 ♀	0.5 ♂		3.3 ♂	1.0 ♂	0.5 ♂	0.3 ♂ 1.3 ♀ 0.3 ♂		1.0 ♂ 0.5 ♀ 0.5 ♂
			2.8j		9.0j	2.5j	2.5j	10.5j	4.8j	4.0j	12.0j	0.8j		2.5j
0.3j	0.5j		0.3j	4.5j		1.3j								0.5j
0.8 ♀					0.5j	0.3j				0.5j				
1.3j		1.0j	3.8j	4.0j	2.0j	3.3j	1.0j		0.3j			0.5j		
									0.3 ♂	0.5 ♂				
0.3j	1.0j					1.0j	5.0j	0.5j	0.8 ♀			0.3 ♀		
0.3j			0.5j	1.0j	0.3j	0.5j			0.3j	0.5j	0.5j	0.2j		0.5j
0.3 ♀														
													1.0j	1.0j
													0.5j	
				0.5j		0.5j				0.5j				
			0.5j			0.3j								
		0.5j												
								1.5j				1.5j		1.5j
19.5	8.0	5.0	18.0	25.0	14.5	17.5	11.5	13.0	18.3	10.5	14.5	7.0	2.0	12.5
79.2	46.9	26.3	73.6	104.7	19.0	76.9	37.7	16.0	78.3	90.0	27.2	58.9	18.5	88.8

diurnal lizards (*Cnemidophorus*, *Phrynosoma*, *Sceloporus*) can be assumed to be taking a random sample of arthropods present in burrows and on the ground surface, a low density of spiders in these strata is indicated. However, ground dwelling spiders are probably principally active at night, and may not be adequately sampled by lizards.

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	L	F	P	L	F	P	L	F	P	L	F	P
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<i>Phidroma</i> <i>tufusatus</i> Keyserling	0.2♂			0.3j	2.0j							
<i>Tmarus angulatus</i> (Walckenaer)	0.8j		0.8j	1.3j		1.0j	1.3j			2.0j		
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<i>Habronatus</i> sp.	1.0j											
unidentified	0.2j		0.3j	1.0j	1.0j		0.3j		0.3j			
<b>ARCIOPIDAE</b>												
<i>Metepeira arizonica</i> Chamberlin & Ivie	0.5j		0.3j	1.7j		0.3j	0.7j	1.0♂	0.3j	2.0j		
<i>Eusata</i> sp.	0.2j					0.3♂						
<i>Hamatalva grisea</i> Keyserling			2.0j			0.8j			0.5j			
<b>DICTYNIDAE</b>												
<i>Dictyna pson</i> Chamberlin & Certsch					1.0j			1.0♂		0.5j		
<b>All species</b>												
Total individuals	16.7	7.0	12.3	11.0	12.0	6.3	6.7	5.0	1.3	3.0	2.0	
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	L	F	P	L	F	P	L	F	P	L	F	P	L	F	P	
	(4)	(2)	(2)	(4)	(2)	(2)	(4)	(2)	(2)	(4)	(2)	(2)	(6)	(2)	(2)	
11.3	4.0	2.5	9.5	15.5	2.0	7.5	1.5	0.5	5.1	2.0		2.8	4.0			
0.3♂	1.5♂		0.5♂			0.3♂	0.5♂		3.3♂	1.0♂	0.5♂	0.3♂	1.0♂	0.5♀	0.5♀	
			0.8♀			0.5♀						2.5♂	0.5♂	0.3♂	0.5♂	
						0.3♀						0.3♀				
			2.8j			9.0j	2.5j	2.5j	10.5j	4.8j	4.0j	12.0j	0.8j		2.5j	
0.3j	0.5j		0.3j	4.5j		1.3j									0.5j	
0.8♀						0.5j	0.3j					0.5j				
1.3j		1.0j	3.8j	4.0j	2.0j	3.3j	1.0j		0.3j	0.5♂			0.5j			
									0.3♂	0.5♂					0.3♀	
0.3j	1.0j					1.0j	5.0j	0.5j	0.3j	0.5j					0.2j	
0.3j				0.5j	1.0j	0.3j	0.5j		0.3j	0.5j	0.5j					
0.3♀															1.0j	1.0j
0.5j						0.5j						1.5j				1.5j
0.5j																1.5j
19.5	8.0	5.0	18.0	25.0	14.5	17.5	11.5	13.0	18.3	10.5	14.5	7.0	2.0	12.5		
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Dr. Herbert Levi, Dr. Willis J. Gertsch and Dr. Robert Schick in making taxonomic determinations of the spiders collected.

### RESULTS

**DENSITY AND BIOMASS.** Table 1 gives the density of spiders in each of the shrub species for each collection. All individuals were weighed together. Total spider density is plotted in figure 1. Densities in the different shrubs show two seasonal highs, one

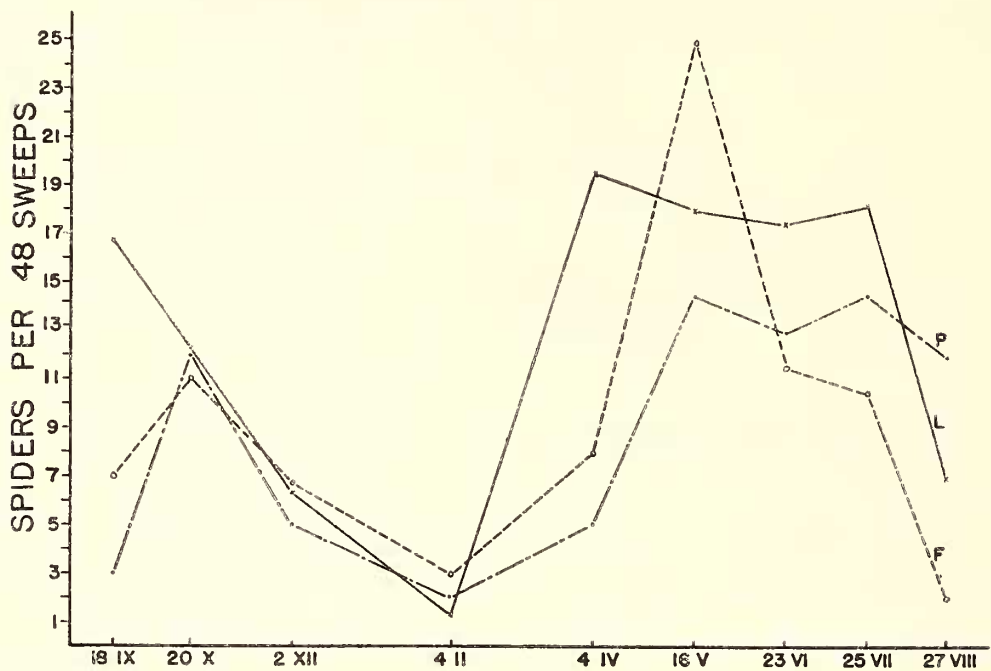


FIG. 1. Seasonal variation in abundance of spiders in the different shrubs. L = creosote bush, *Larrea divaricata*; P = mariola, *Parthenium incanum*; F = tarbush, *Flourensia cernua*.

in the period from April through July, and the second in October. The latter peak is much smaller and more limited in time, and possibly does not occur for creosote bush, which may have only one period of spider abundance, from April through September. The patterns for the three shrubs are somewhat different. Densities in creosote bush remained at almost the same high level from April through July; the spring-summer plateau did not develop in mariola until May, but was sustained through August, while tarbush showed a very sharp peak density, exceeding the other shrubs, in mid May.

The standing biomasses of spiders per square meter of plant cover are plotted for each collection period in figure 2. Figure 3A presents density and biomass per hectare of habitat, which takes into account the relative coverages of the three shrubs. The per hectare figures are therefore dominated by the density

values for creosote bush, which provides 83.8 per cent of the total shrub cover, and *Misumenops* spp. which form 51.8 per cent of the total spiders collected. The numerical dominance of *Misum-*

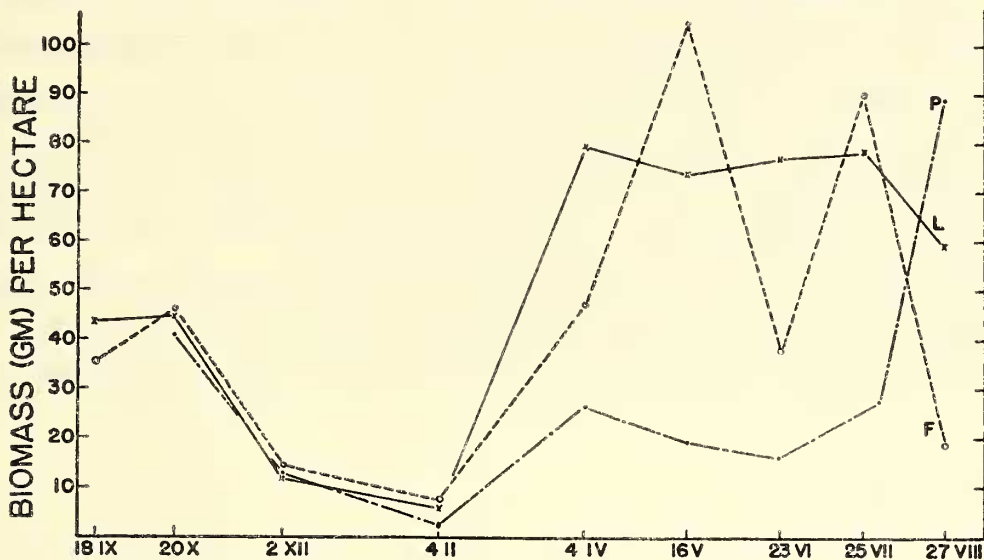


FIG. 2. Seasonal variation of biomass of spiders in different shrubs. L = creosote bush, P = mariola, F = tarbush.

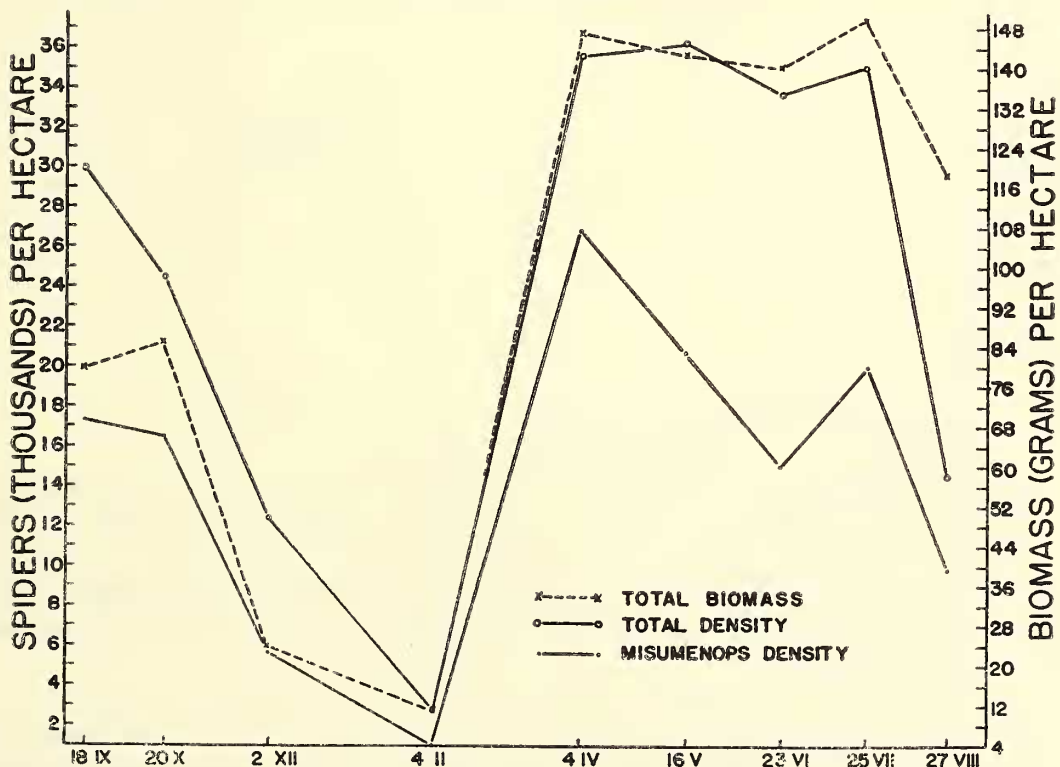


FIG. 3A. Seasonal variations in habitat density and biomass of spiders, and of *Misumenops* spp.

*enops* is shown by the curve for it alone; seasonal densities of the other spiders are shown in figure 3B, using a magnified abundance scale.

Certain anomalies between the density curve (figure 1) and

biomass curve (figure 2) are largely due to changes in the age structure of the *Misumenops* populations, particularly the number of heavy adults in comparison to the lighter juveniles, and to the plant distribution of the adults. For example: (1) For creosote bush on 18 August, when density was high but biomass only moderate, there were 54 juvenile *Misumenops* for each adult. By 20 October, when density had declined though biomass was almost unchanged, there were 28 juveniles: 7 adults. The decline in numbers (of juveniles) was compensated by the greater weight of the then more numerous adults. (2) The increase in the spider biomass in mariola, which increased from a continuously low level to a sudden maximum in August, was due to the presence

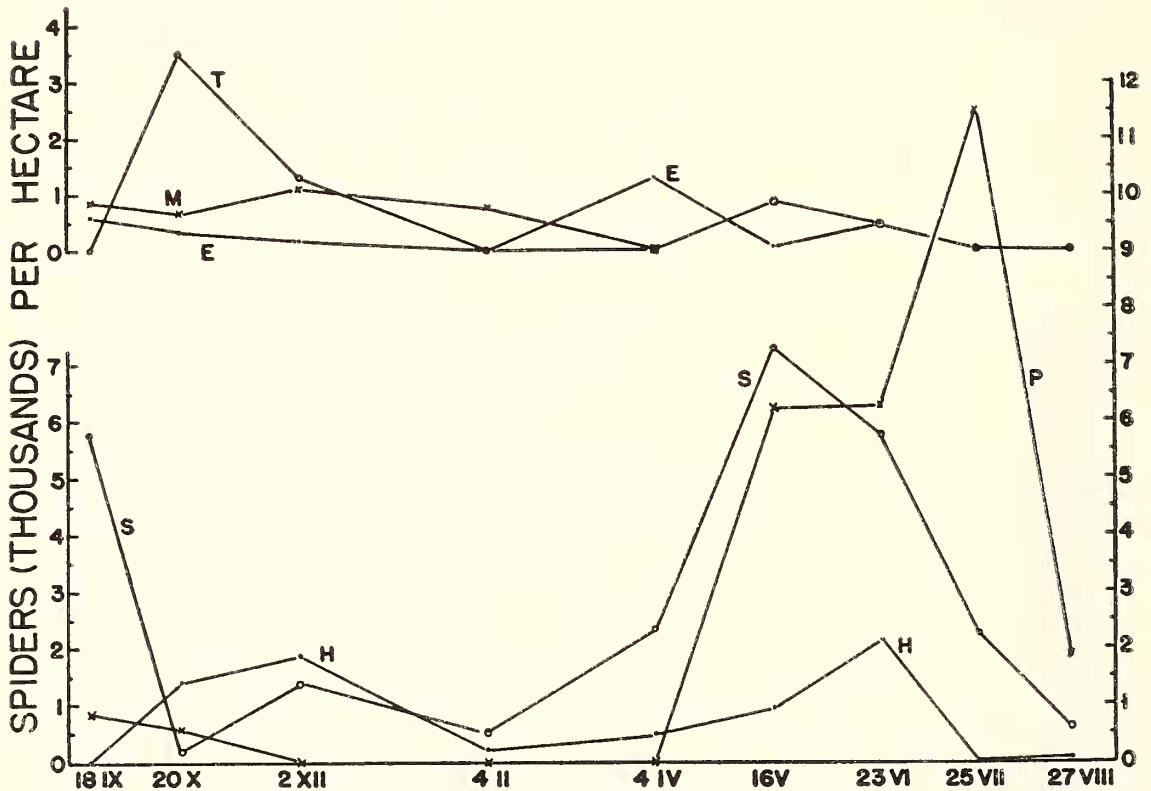


FIG. 3B. Seasonal variations in density of individual species of spiders. Upper graph: E = *Ebo* spp.; M = *Metepeira arizonica*; H = *Hamataliva grisea*. Lower graph: P = *Philodromus infuscatus*, S = *Sassacus papenhoei*, T = *Tmarus angulatus*.

of adult *Misumenops*, not previously present in this shrub, although present on the other two shrubs. The total biomass of spiders (figure 3A) follows rather closely the total density.

SEASONAL DISTRIBUTION AND CLIMATIC FACTORS. The minimum density of spiders in the shrub stratum occurred in February, coincident with the period of lowest air temperatures (figure 4). The lesser depression in density, through August and into September came at the end of the period of sustained high summer



temperatures, when air temperature was declining and air humidity increasing. Highest temperatures and lowest humidities occurred in early June.

SEASONAL DISTRIBUTION AND CONDITION OF THE SHRUBS. The periods of blooming and leaf bearing of the three shrubs, and the seasonal variation in density of the three most abundant species of spiders in these shrubs, are shown in figure 5.

*Misumenops* spp. are consistently present on the evergreen creosote bush, except during the period of lowest winter temperatures. The plateau density is established in April, at the time of the spring blooming of the creosote bush. In tarbush the maximum *Misumenops* density is a very sharp peak, occurring in mid

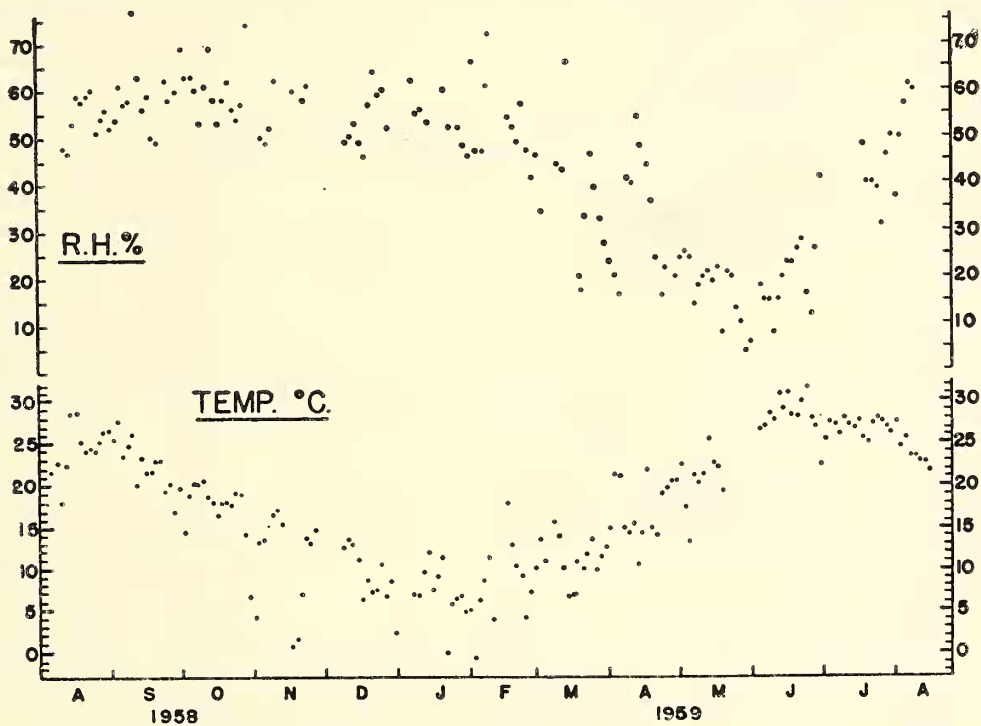


FIG. 4. Air temperature and relative humidity recorded in center of study area.

June, in the first month of full leaf bearing of this deciduous shrub. There is no significant response of density to the blooming period, October–November, of tarbush. For mariola the highest densities are recorded in August and October (no collection in September), both within the blooming period. August was the only time when mature *Misumenops* were found on mariola, and then both species were present.

*Philodromus* was present abundantly only on mariola, and during the first half of the leaf-bearing period. Density declined in August during the period of blooming, when *Misumenops* became abundant.

*Sassacus* densities were highest, on all plants, in the period April–June.

DISTRIBUTION ACCORDING TO PLANTS. An analysis of variance of the densities of the more abundant spiders on the three species of shrubs showed that there are significant differences attributable to plant species. (1) The density of *Misumenops* spp. on creosote bush is significantly greater than that on mariola. There is no difference between creosote and tarbush, or tarbush and mariola. (2) The abundance of *Tmarus angulatus* is highly significantly greater on tarbush than on creosote bush ( $p < 0.001$ ),

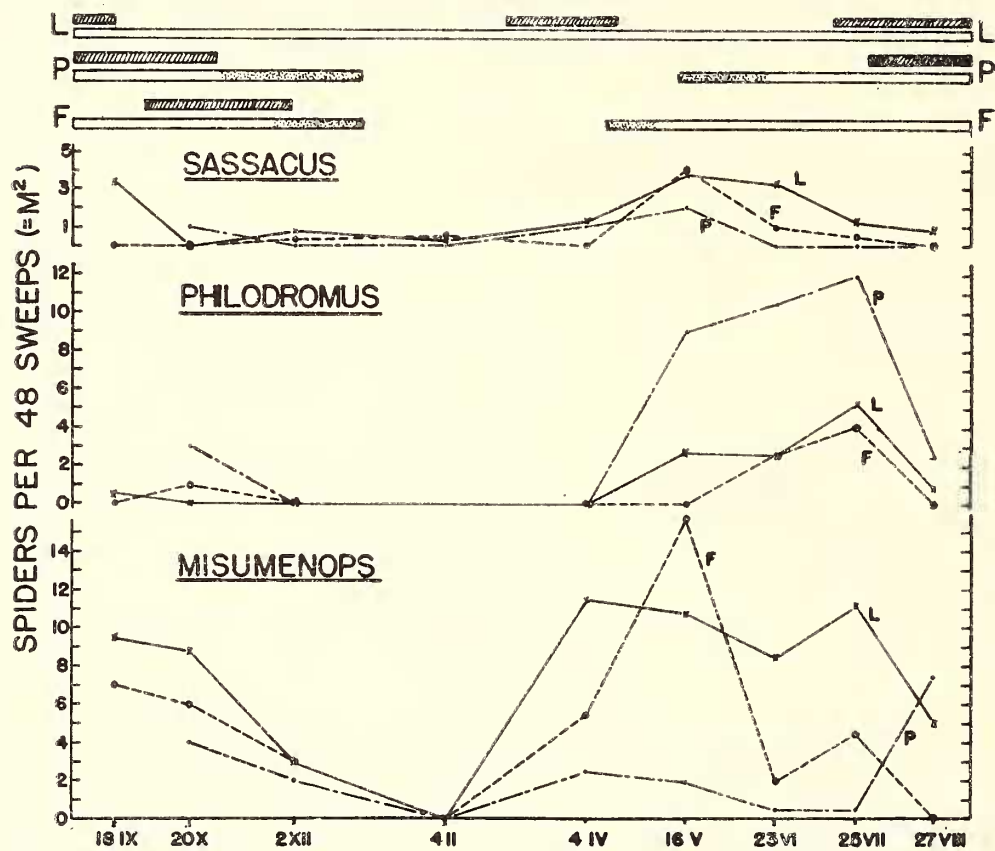


FIG. 5. Variation in abundance of three spiders in the different shrubs, according to the development of these shrubs as shown in the upper bar graphs. L = creosote bush, P = mariola, F = tarbush; cross hatched bars = time of blooming, dotted bar = time of development of leaves or shedding of leaves, plain bar = period of full leaf, no bar = no leaves.

and it was never taken on mariola. (3) The abundance of *Philodromus infuscatus* is significantly greater on mariola than on creosote bush and tarbush. There is no difference between the last two species. (4) *Sassacus papenhoei* and *Phidippus* sp. densities are not significantly different on different shrubs.

Simple inspection of the data in table 1 indicates that the orb-

weavers, *Metepeira arizonica* and *Eustala* sp., are probably distributed independent of plant species, while *Dictyna peon* was taken only on mariola, with one exception, and *Hamataliva grisea* only on creosote bush.

SEASONAL OCCURRENCE AND INSECT BIOMASS. The insect and spider biomasses per 48 sweeps are given in Table 2, according to species of shrub and time of collection. For creosote bush and tarbush, the insect : spider biomass ratios are clearly highest during periods of low spider biomass, and lowest during periods of highest biomass. The largest ratios occurred in February, when insects were still present in the shrubs, while spiders were largely absent. In several cases the spider standing biomass equalled or was larger than the insect biomass.

TABLE 2. COMPARISON OF INSECT AND SPIDER STANDING CROP BIOMASSES PER 48 SWEEPS OF EACH SHRUB SPECIES. Biomass in mgm.

Date	Insect biomass/spider biomass or prey/predator biomass ratio		
	creosote bush	tarbush	mariola
18 Sept. 1958	142.4/43.6 = 3.3	274.4/35.5 = 7.7	
20 Oct. 1958	147.0/44.5 = 3.3	184.6/46.2 = 4.0	162.7/40.9 = 4.0
2 Dec. 1958	36.8/11.8 = 3.2	250.4/14.3 = 17.7	96.3/12.5 = 7.7
4 Feb. 1959	1108.5/5.7 = 195	652.8/7.4 = 88.3	84.7/2.5 = 33.9
2 April 1959	171.0/79.2 = 2.2	723.0/46.9 = 15.4	46.9/26.3 = 1.8
16 May 1959	132.2/73.6 = 1.8	334.3/104.7 = 3.2	53.5/19.0 = 2.8
23 June 1959	107.0/76.9 = 1.4	130.6/37.7 = 2.8	15.6/16.0 = 1.0
27 July 1959	78.0/78.3 = 1.0	152.5/90.9 = 1.7	69.9/27.2 = 2.6
27 Aug. 1959	43.3/58.9 = 0.74	135.1/18.5 = 7.3	226.0/88.8 = 2.5

#### DEVELOPMENT AND REPRODUCTION

1. *Misumenops dubius* and *M. coloradensis*. As shown in figure 6, both these species had a maximum abundance of mature individuals in late July. However, mature *coloradensis* occurred only in June–July–August collections (except one individual in October), while mature *dubius* were present April through October.

Since it is not possible to distinguish the juveniles of these two species, all *Misumenops* are plotted together in the size distributions of each collection (figure 7A). This plot shows that:



(1) As indicated by the seasonal spread of mature individuals, and the considerable size range in each collection, reproduction takes place throughout a considerable part of the year. But, most breeding must have occurred in July and August when mature individuals comprised 60 per cent and 56.5 per cent of the total numbers respectively.

(2) Penultimate instar males, recognized by partial development of the palpi, were present in October, April–June and August, with the majority in April–June, i.e. preceding the appearance of most of the mature males. Penultimate instar females could not be recognized with certainty.

(3) Eggs were probably laid in late July and August. The

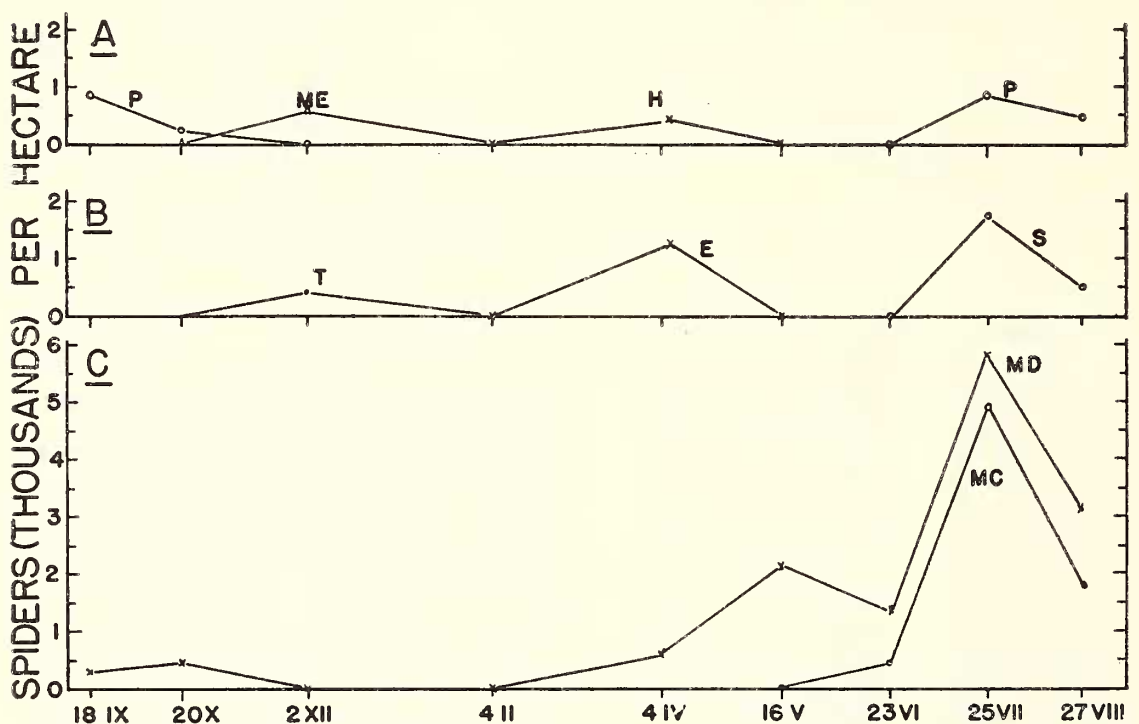


FIG. 6. Density of mature individuals of different spiders. A: P = *Philodromus infuscatus*, ME = *Metepeira arizonica*, H = *Habronattus* sp. B: T = *Tmarus angulatus*, E = *Ebo* spp., S = *Sassacus papenhoiei*. C: MD = *Misumenops dubius*, MC = *Misumenops coloradensis*.

smallest individuals, of the 2nd and 3rd instars, were present in numbers only in August–October.

(4) There was a gradual disappearance of *Misumenops* from the shrub stratum from November through January, until there were none present in February. The disappearance probably is a migration from the shrubs downward into sites of hibernation. *Misumenops* overwinter as juveniles in various instars.

(5) *Misumenops* suddenly reappeared in the shrub stratum in

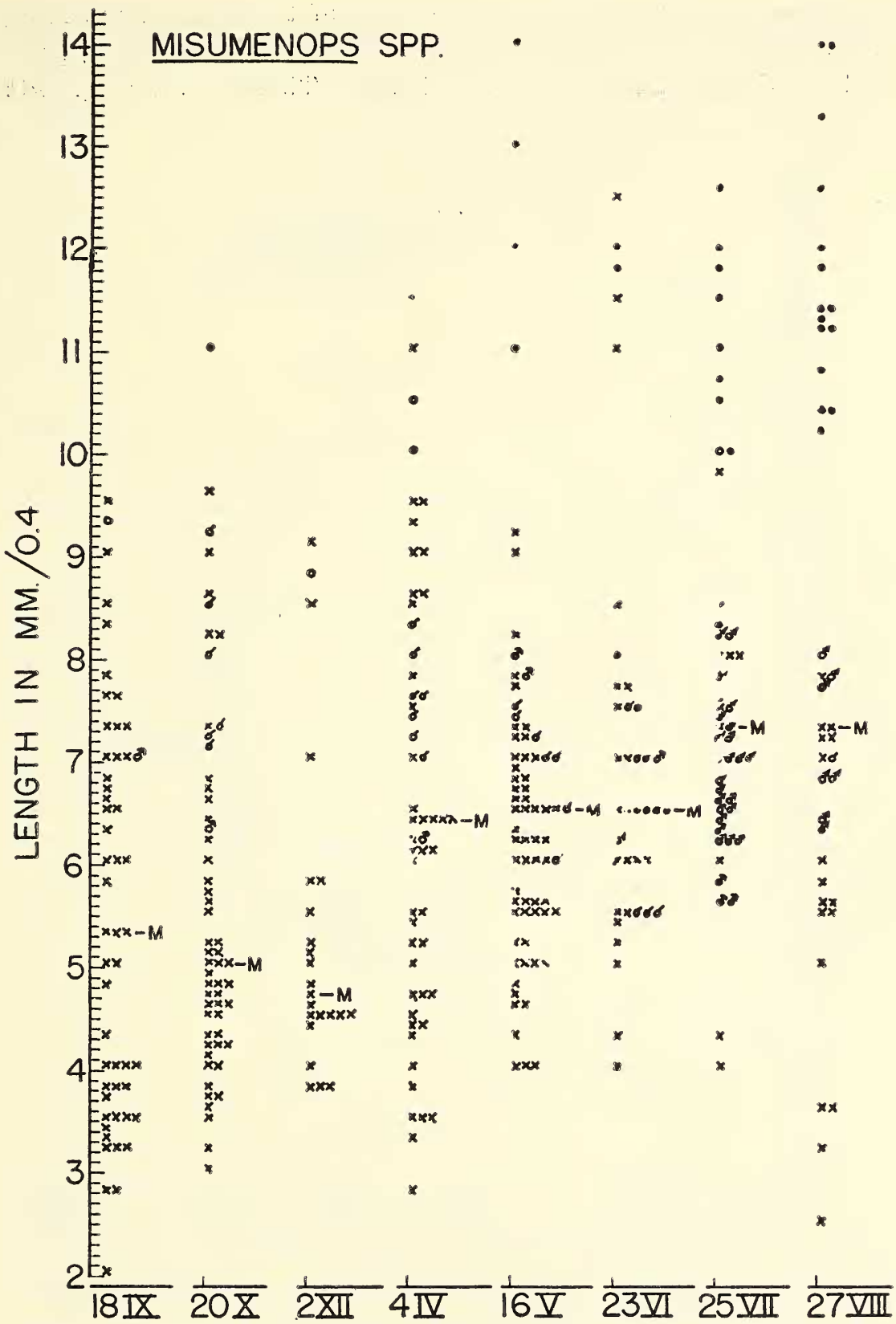


FIG. 7A. Size distribution of individuals of *Misumenops* spp. in the different collections. (No individuals taken 4 II). x=juveniles, ♂=mature males, ♂=penultimate males, •=mature females, o=penultimate females, M=mode.

numbers in early April, with the mode of the populations being about two instars larger than in November and December, prior to their disappearance from the shrubs. There was then growth

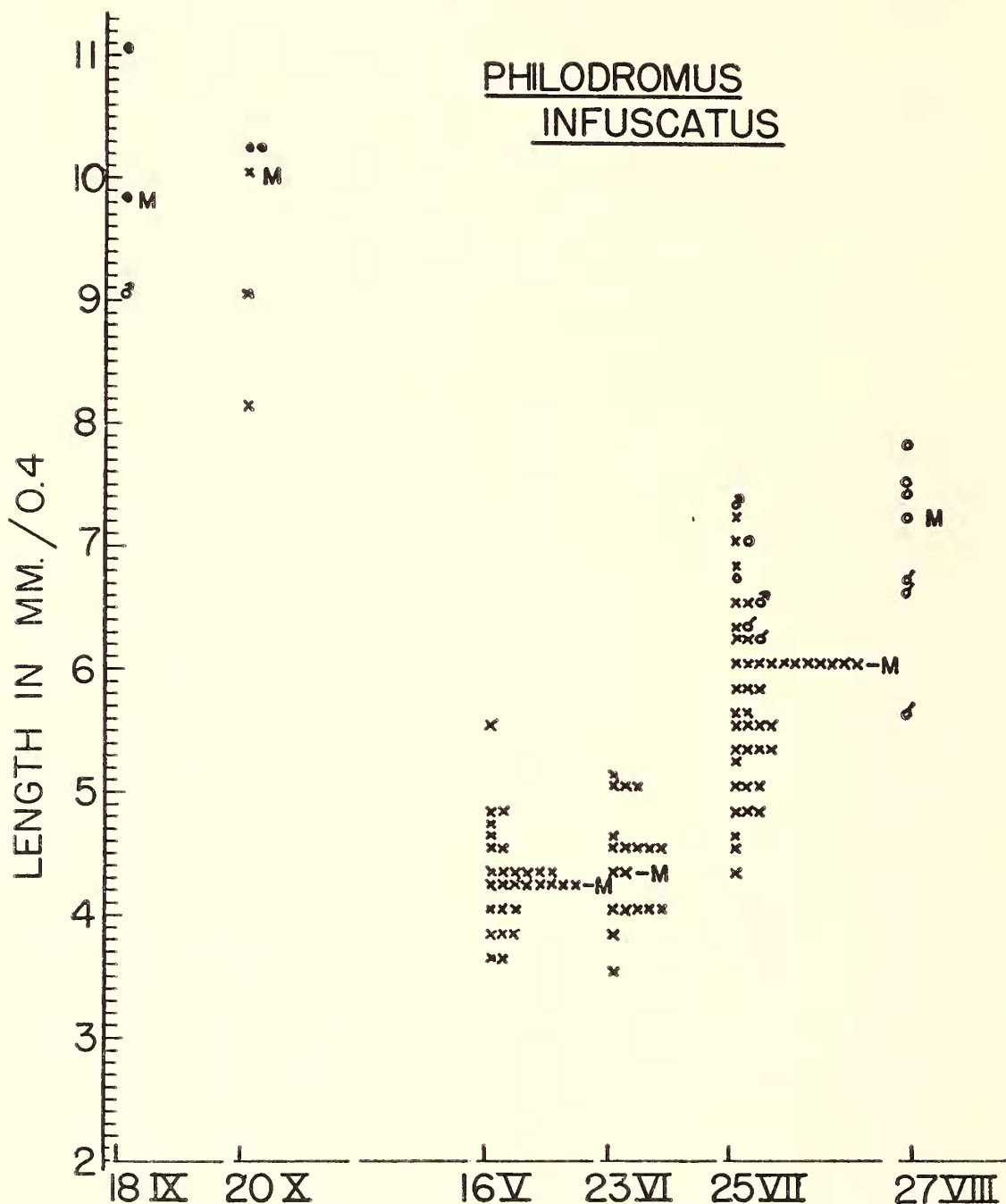


FIG. 7B. Size distribution of individuals of *Philodromus infuscatus* in the different collections. (No individuals taken in collections of 2 XII, 4 II and 4 IV). Symbols as in fig. 7A.

and maturation, with little attrition of the populations, through the penultimate instar to the mature instar in July and August.

When all individual *Misumenops* were placed together in a



single frequency distribution plot, it was possible to recognize what are probably instar groupings, as follows:

Instar	<i>M. dubius</i>	<i>M. coloradensis</i>
1st	spent in egg sac	spent in egg sac
2nd	1.13 mm.	1.01 mm.
3rd	1.42	1.30
4th	1.82	1.62
5th	2.23	2.02
6th	2.83	2.51 (most mature ♂♂ here)
7th	3.65	3.16
8th	4.66	4.05 (most mature ♀♀ here)

Mature *M. dubius* were significantly larger than *M. coloradensis*.

This instar reconstruction assumes that climatic conditions and other factors that vary with the seasons have no effect on the size of an instar, although they may influence the duration of the instar. Jones (1941) found that temperature and humidity changes had little effect on the length of cephalothorax of *Agelena naevia*. The number of molts interpreted is more than to be expected in general for spiders of this size, and compares to 6 molts for both males and females in *Misumena vatia* and *M. aleatoria* (Bonnet, in Deevey 1949). However, the ratio of increase from one instar to the next was 1.25–1.28, in agreement with Bodenheimer (1933) and Jones (1941) for other species of spiders.

II. *Philodromus infuscatus* (figure 7B) shows a rather clear picture of the simultaneous development of one generation per year. The eggs were probably laid in September and October, when mature individuals formed 2/3 rds of the total collections of this species. Mature *P. infuscatus* persisted in numbers longer than *Misumenops dubius*. *P. infuscatus* disappeared from the shrub stratum for the extended period of November through April, and may overwinter in the egg sac or as very young instars. Collections from May onward showed a steady increase in the modal size of the population, with the first penultimate instar individuals appearing in July. Penultimate females are recognizable by the beginning development of a brown color pattern on the grey dorsum of abdomen and thorax, which is only weakly if at all present in mature males. In August only penultimate individuals were present; apparently there was considerable attrition of the population in the previous month. These individuals reached mature condition in the next two months.

III. *Sassacus papenhoei* (figure 7C) shows a development similar to *Philodromus*, but with certain important ecological differences. Reproduction probably occurred in July and August, as penultimate females and mature males were taken in these months. From September through June there was a clear

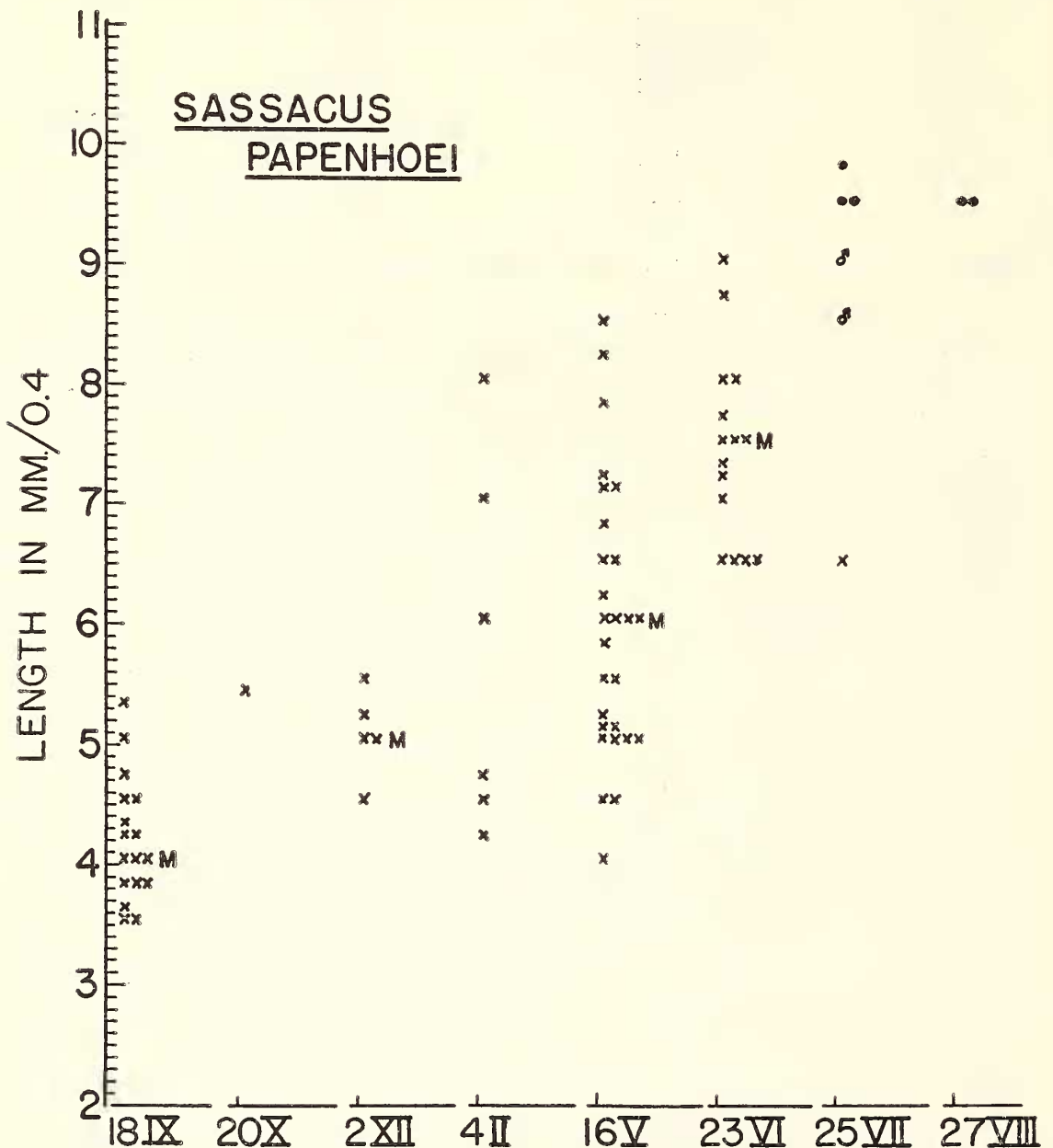


FIG. 7C. Size distribution of individuals of *Sassacus papenhoei* in the different collections. Symbols as in fig. 7A.

linear growth of the individuals, with their continuing presence, though in reduced numbers, through the winter.

*Tmarus angulatus* probably breeds in May, with the first individuals of the new generation appearing in June. Very few individuals were taken during the summer (none at all in July and September). This may represent an estival migration from the

shrub stratum, or the younger instars may have different ecological preferences. Individuals of this species were present in the shrubs all through the winter, as fairly large juveniles. Penultimate males were first present in May. The one mature female, taken in December, is probably a post-reproductive survivor.

The size distribution and seasonal distribution of *Phidippus* sp. and *Habronattus* sp. was very irregular and could not be interpreted clearly. These may be primarily ground dwelling species, which irregularly enter the shrub stratum.

Captures of a few mature individuals of other species suggests (as plotted in figure 6) that *Ebo albocaudatus* and *E. parabolis* and *Habronattus* sp. reproduce in April, while *Metepeira arizonica* and *Dictyna peon* reproduce in late December.

## DISCUSSION

### NATURE OF THE FAUNA.

The spider fauna of the present desert shrub community is clearly one that is dominated by only a few species of spiders that ambush or actively hunt their prey rather than snare it. Two species of the same genus, *Misumenops*, comprised 52 per cent of the individuals collected, and 68.5 per cent of the calculated habitat densities. These species of *Misumenops* show the characteristic of ecological dominants (within their size and trophic groupings) of the longest persistence of numbers and of reproduction throughout the year. The numerical subdominants were *Philodromus infuscatus* (16.7 per cent of collections), *Sasacus papenhoei* (10.6 per cent) and *Tmarus angulatus* (4.7 per cent). These five species thus formed 85 per cent of the total number of individuals. Of the 20 species collected, only 11 exceeded one per cent of the collection; 7 species were represented by only 1 or 2 individuals. Web-spinning families (Argiopidae, Dictynidae, Micryphantidae) comprised only 6.1 per cent of the individuals and 6 of 20 species.

This fauna for a southern desert shrub community is quite similar to that found by Fautin (1946) for several associations of the northern desert shrub biome. Fautin found a total of 23 species in four different plant associations, but only 10-19 in any particular association. Of these species, only 4 are mentioned as being quantitatively important: *Philodromus* sp. and *Misumenops celer* (Hentz) (Thomisidae), *Dendryphantas* sp. (Salticidae)



and *Metepeira foxi* Gertsch and Ivie (Argiopidae). There are one species (*Sassacus papenhoei*) and 8 genera in common between these northern and southern collections; two of the common genera, *Misumenops* and *Philodromus*, are numerical dominants in both situations. Fautin collected in both the ground and shrub strata, but does not mention any spiders as being important parts of the ground level society of organisms. In analyses of stomach contents of six species of lizards, he found spider remains occurred with a frequency of 0 to 35.3 per cent, and formed up to 6.6 per cent of the total volume.

The number of species found in these desert studies compares with 17, 31 and 18 species respectively for the beach, foredune and cottonwood seral stages of Lake Michigan sand dune vegetation (Lowrie 1948), 168 for oak subclimax and 122 for beech-maple climax (Lowrie 1948), 39 species for the oak-hickory sere (Dowdy 1950), 139 species (only 30 of which exceeded 1 per cent of the collections) in oak-hickory river terrace forest (Gibson 1947), and an average of 23 species for stands of *Andropogon* (Barnes and Barnes 1955). Direct comparisons of species numbers is impossible because of differences in intensities of collecting and thoroughness of examining different strata in these studies, but it is apparent that the richness of the spider fauna increases with the plant density of the habitat and the degree of stratification. The limited variety of the spider fauna of desert communities, and of the roughly analogous sand dune habitats, is probably due to the low plant density and limited stratification in these situations. A desert community has only ground and shrub strata, with a very temporary herb stratum.

**HUNTING VERSUS WEB-SPINNING SPIDERS.** As has been nicely shown by Lowrie (1948), hunting spiders predominate in the early stages of succession in deciduous forest and gradually give way to web-spinners towards the climax stage. In the sand dune sere to beech-maple climax, hunting spiders decreased from 71 per cent to 52 per cent of the total species. Dowdy (1950) found 23 web-spinners to 16 hunting species in oak-hickory forest, while Barnes and Barnes (1955) found a ratio of 3 hunting : 2 web-spinning species, and a ratio of 28 : 25 individuals in each category, in the *Andropogon* seral stage of oldfield succession. Desert communities show the most extreme ratio of any situation yet studied (for herb, tree or shrub stratum); the present study



shows a 15 : 4 species ratio and a 50 : 3 individual ratio, and Fautin (1946) found a 16 : 7 species ratio.

In desert communities the low density of shrubs means that there are few situations for web construction. Although desert shrubs provide adequate scaffolding for webs, the windiness resulting from daily extreme temperature changes makes webs very temporary structures. The wind directly damages webs and also destroys them by flexing the branches of the shrubs to which the webs are attached. The branches of creosote bush are particularly flexible and this probably makes this species of shrub least satisfactory, of the three species in the present study, for web spinning. Although web spinning spiders may be conspicuous in a desert community, such as *Araneus carbonarius* in sagebrush (Fautin 1946), it may be that the inefficiency of the temporary webs in capturing food permits the development of only a low population density. It may also be that the predator pressure of spider-hunting wasps may fall more heavily on the orb-weaving spiders than on other types, particularly in habitats with open vegetation (see Rau 1935).

Early stages of deciduous forest seres, like desert communities, have a minimum plant density and stratification, and maximum of air movement for all stages in the sere.

#### GEOGRAPHICAL DISTRIBUTION OF THE ABUNDANT SPECIES

Of the five most abundant species, four are representatives of genera which are strictly western hemisphere (*Misumenops*, *Sassacus*) or predominantly so (*Tmarus*), with possible South American origins; only one species is of a genus (*Philodromus*) which is predominantly palearctic and eastern hemisphere in its affinities.

*Misumenops*, as reviewed by Gertsch (1939), is a discrete genus of the Misumeninae. None of the 11 North American species is apparently congeneric with the species assigned to this genus from the eastern hemisphere. The North American species tend to be limited to southern United States, or at least are more abundant towards the south, especially towards the southwest. Only *M. asperatus* is an exception, being rarer towards the south. *Misumenops coloradensis* Gertsch, 1933, has been reported only from the southwestern states; *M. dubius* (Keyserling, 1880) has

been reported all along the southern tier of states. No ecological data are available for either of these species.

With regard to other species of *Misumenops*, *M. asperatus* was found as a dominant in black oak forest (Lowrie 1942), and was present in the herb and shrub strata of beech-maple forest (Elliott 1930) and all forested parts of an oak-hickory river terrace (Gibson 1947). *M. celer* was found to be typical of the upper strata of the same river terrace, and was present as a numerical dominant in sagebrush (Fautin 1946). *M. oblongus* was found to be typical of forest borders (Gibson 1947).

In addition to the North American species, Bonnet (1957) lists 31 species from South and Central America which do not get into southwestern United States.

*Philodromus* (148 species listed in Bonnet 1958) is found on all continents, but principally in the nearctic and palearctic regions. Gertsch (1939) gives 53 species as palearctic, 40 as nearctic and 3 as holartic.

*P. infuscatus* Keyserling, 1880, is generally distributed throughout the United States and Canada, however there seem to be no published observations on its autecology. Several other species are also found in southwestern United States; *P. virescens* is common on sagebrush (Fautin 1946, Gertsch 1949). Species of this genus are found only on, or predominantly on vegetation. *P. placidus* was not found until the shrub subclimax stage in the maritime communities of North Carolina (Barnes 1953).

*Tmarus* (103 species listed in Bonnet 1959) is found principally in South America, with only 6 nearctic and palearctic species. Five species are reported from the United States. *Tmarus angulatus* (Walckenaer, 1837) is generally distributed throughout the United States and into Mexico. Elliott (1930) reports this species as a true forest form, in the herb and shrub strata of beech-maple forest. *T. rubromaculatus* is found in the shrub subclimax of maritime communities in the southeast (Barnes 1953). The other United States species are southeastern in their distribution.

*Sassacus* (14 species listed in Bonnet 1958) is found only in the western hemisphere. Of the 6 species reported for the United States, only *S. papenhoei* Peckham, 1895, has a general distribution. Fautin (1946) reports it from the greasewood fasciation of the northern desert shrub biome.



## COMPARATIVE ABUNDANCE

In the present study, spider densities averaged 10.8 individuals (range 1.2–25.0) per 48-sweeps, for all three species of shrubs combined, and 13.0 per 48-sweeps of creosote bush only. Habitat densities ranged through the seasons from 2800 to 36,300 spiders per hectare, with an annual average density of 24,900 spiders per hectare. These values are quite a bit higher than those found by Fautin (1946) for communities within sagebrush desert, i.e. annual average densities of 1.2–5.4 spiders per 50-sweeps of shrubs, or (calculated from his data) 1340 to 9740 spiders per hectare of the different habitats. Shrub coverages were almost the same in these two desert areas.

As expected, these densities for desert communities, on a hectare basis are lower than densities for more densely vegetated communities. Fichter (1954) found densities, changing through the seasons, of 0 to 250,000 spiders per hectare of the herb stratum in upland true prairie. Weese's data (1924) indicate about 58,000 to 165,000 spiders per hectare, for the lower strata (soil through shrubs) of elm-maple forest. Bristowe (1939) found 280,000 to 918,000 spiders per hectare in undisturbed fields of cock's foot grass (*Dactylis*).

Bristowe (1941) discusses the importance of habitat density to success of mating in spiders.

There seem to be no comparative data in the literature on biomass of spider populations.

## FACTORS IN SEASONAL CHANGES IN ABUNDANCE OF SPIDERS

**LOW WINTER TEMPERATURES.** All species showed a reduced abundance in the shrub stratum in the winter months, January–March, when air temperatures were the lowest for the year. This undoubtedly represents a migratory movement out of the more exposed shrub stratum into the soil litter (very sparse in the study area) and into burrows and crevices in the soil. Such migration is well established for spiders and other arthropods in deciduous forest (Dowdy 1951), and has been attributed particularly to temperature changes (Elliott 1930). *Misumenops* spp. and *Philodromus infuscatus*, the most abundant forms on an annual basis, are completely absent from the shrubs in winter, *P. infuscatus* for the extended period of November through April.

*Misumenops* overwinter as juveniles, while *Philodromus* probably does so in the egg sac. *Ebo* spp. and *Hamataliva grisea* are also absent in the wintertime.

The other species persisted in the shrubs during the winter, though at a reduced level, except *Tmarus angulatus*, which reached a seasonal maximum in December when air temperatures were only slightly above the January–February minimum. Apparently there are species differences in response to low temperature. Kuenzler (1958) found that several species of *Lycosa* stay in their burrows when the temperature is below 10° C., and are less active after 2 a.m., possibly because of the lower temperatures then.

SUMMER HIGH TEMPERATURE AND LOW HUMIDITY. Maximum air temperatures and minimum humidities coincided in June. Humidity and temperature were moderated in July and August by the occurrence of rains.

A depressing effect of this combination of temperature and humidity may possibly be seen in the June depression of the *Misumenops* populations, and the fact that the peak abundances of other species occur either after (e.g. *Philodromus*) or before (e.g. *Sassacus*) this time. *Tmarus* is the unusual exception in that a peak of abundance was recorded for it in June.

Spiders are rather tolerant of high temperatures. Holm (1950) found that the ground dwelling spiders in Swedish Lapland had thresholds of heat paralysis as follows: 5 species less than 37° C., 11 species 37–38.9°, 16 species 39–40.9°, 14 species 41–42.9°, 11 species 43–45° and 15 species over 45°. Lowrie (1942) found that two lycosids could tolerate 30 minutes on a surface at 45° C. So, it is probable that the temperatures in the present study area never exceeded the limits of tolerance of the species. However, temperature responses and preferences may be very important in determining microhabitat distribution, and the effects of nonoptimum temperatures in altering activity and development can be important in determining the success of different species in a particular area.

Nørgaard (1951) found a very clear difference in the temperature preferences and tolerances of two lycosids of Danish sphagnum bogs. *Pirata piraticus*, which stays within the sphagnum mat, preferred temperatures of 18–24° C. and showed heat stupor at 35.3°, while *Lycosa pullata*, which is active on the surface of



the mat, and in the sun, chose temperatures of 28–36° and did not show heat stupor until 43.0° C. Holm (1950) found some relationship between the biotope distribution of different species and their temperatures of heat paralysis. Barnes and Barnes (1954) found that the spider fauna of thick beach drift in *Spartina* vegetated areas is characteristically quite different from that in the thin drift on sand beaches; this difference was attributed to the relatively “mesic” and “xeric” microclimatic conditions in the two types of drift.

Response to humidity is insignificant in relation to the response to temperature (Nørgaard 1951). In a limited number of experiments with humidity gradients, Weese (1924) found only weakly expressed preferences: *Acrosoma spinea* (Argiopidae) and *Dendryphantes aestivalis* (Salticidae) tended to select the driest part of a wet-medium-dry gradient; *Epeira gibberosa* (Argiopidae) selected the medium and wet part of the gradient; and, *Anyphaena* sp. selected the wet.

Humidity is probably important only as it interacts with temperature to influence evaporative water loss. Davies and Edney (1952) found that spiders are not far behind insects in their ability to withstand desiccation, and probably have a wax waterproof coating similar to that in insects. Water loss is reduced by closure of the spiracles to the lungs for much of the time. Temperature has little effect on evaporation, up to a critical temperature, when there is a sharp upward break in the rate of evaporation curve. Critical temperatures found for four species, none of which can be considered adapted to xeric conditions, were: over 40–42° for *Meta segmentata* and *Tegenaria derhami*; approximately 40–42° for *Lycosa amentata*; and, approximately 34–36° for *Zilla atrica*. Clearly there are species differences in the rate of desiccation, and possibly in the tolerance of desiccation. Nørgaard (1951) found that *Pirata piraticus* died much more quickly of desiccation than *Lycosa pullata*. *Dolomedes urinator* dies without water in 4 hours, while *Latrodectus mactans* can live on only the water in its prey (Lowrie 1942). Nemenz (1954) measured the rate of evaporation at 25° C. and 30 per cent relative humidity, and found tremendous interspecific differences, ranging from 2–5 per cent of the initial body weight per day (usually after a higher loss the first day) in *Agelena*, *Tegenaria*, *Aranea* and *Theridion* spp., to 12–28 per cent the

first day for *Dolomedes fimbriatus*, and 30–80 per cent the first day for *Agryoneta aquatica*. He concluded that water loss, influenced by a complex of microenvironmental factors, may well influence the biotope distribution of spiders. In an overall study of water balance, Nemenz (1954) found that: (1) no water vapor is taken up through the body surface, (2) all spiders drink when their water deficit becomes great enough, replacing 89–94 per cent of their water loss, (3) the principal loss of water is through the body surface, with loss from the lungs only 1/70th to 1/80th of total loss, (4) no hygrotaxis can be demonstrated, and in gradient experiments there is a preference for intermediate humidities.

Browning (1941), Jones (1941) and Weese (1924) give data from experimental studies on the effect of humidity and temperature on development.

Because of the general resistance of spiders to desiccation, and the different rates of water loss in different species, it is probable that desert environments are not too extreme for many species, but the stress of desiccation, as it limits survival and reproduction, particularly when food (= water) supply is low, probably is an important factor in determining the outcome of interspecific competition.

PLANT DEVELOPMENT. Presence and abundance of spiders in the present study showed some relationship to the state of development of the different shrubs, probably because of the effect of the latter on the productivity of herbivorous arthropods, i.e. the food supply of the spiders. (1) *Misumenops* showed the most stable density in creosote bush, which is evergreen. A high density was immediately established in this shrub as soon as the winter temperatures began to moderate. This also was the time of the spring blooming of this shrub, which would be advantageous to an ambushing spider preying on insects attracted to flowers. (2) *Philodromus*, which has a definite preference for mariola, did not appear until May, when this shrub was beginning to leaf out, after entirely shedding its leaves in the winter. (3) The peak density of *Misumenops* in tarbush did not occur until June, after these shrubs had reached full leaf. (4) *Misumenops* did not have moderate or high densities in mariola except in August to October, which is the period of blooming of this shrub.

FOOD SUPPLY. AMOUNT. The relationship between the num-



bers of arthropods and spiders has been reported in the literature as follows: in shrub stratum of sagebrush deserts, spiders 2.4–8.5 per cent of total arthropods (Fautin 1946); in meadow, spiders 17.1 per cent of total (McAtee 1907); in prairie, spiders 5.8–7.8 per cent of total (Muma and Muma 1949); in the herb stratum of elm-maple forest, spiders 10.2 per cent (Rice 1946) and in maple-red oak sere, 13.9 per cent (Smith-Davidson 1932).

Comparison of numbers of organisms in different trophic levels is often not of much significance, if there are differences in their size and productivity. However, for comparative purposes the present data were calculated in this form. Spiders formed a highly variable part of the total arthropod collections: for creosote bush, 0.12–47.3 per cent, for tarbush, 0.03–37.9 per cent, and for mariola, 0.92–49.8 per cent. The very low percentages were due to large numbers of chermids and/or lace bugs present in certain collections. Average percentages, excluding the latter collections, were: creosote bush, spiders 26.6 per cent of total arthropods, tarbush, 31.0 per cent, mariola, 39.7 per cent. These values are considerably higher than any previously reported.

Assuming that insects are the only food supply of spiders, and that all species of insects are potential prey (excepting those individuals too large for capture, which are omitted in the present calculations), the predator/prey ratios in the present study are: (1) for creosote bush, 36.3 per cent on the basis of individuals and 47.2 per cent on a basis of biomass (from Table 2), (2) for tarbush, 44.9 and 13.3 per cent, (3) for mariola 42.3 and 31.3 per cent. Biomass ratios are even higher if one uses only those groups of insects that are the most likely prey of crab spiders and jumping spiders.

Odum (1959) gives primary consumer/secondary consumer biomass ratios of 8.3 to 36.4 per cent for various fresh water and terrestrial communities. Since the efficiency of conversion from herbivore biomass to carnivore mass is probably 10 per cent or less in general, the herbivorous insects resident in the desert shrubs must have a much higher rate of production than the spiders, in order to serve as the food supply sustaining the latter. The sedentary ambushing spiders in the present study (*Misumenops* spp.) must also benefit to some extent from insects attracted to flowers of these shrubs, but not resident in the shrubs, and thus poorly sampled in the sweeps.

TABLE 3. ANALYSIS OF ARTHROPOD BIOMASS IN CREOSOTE BUSH SWEEPS. Biomass as mg./48 sweeps, percentages as percent of total insect biomass.

	18 Sept.	20 Oct.	2 Dec.	4 Feb.	2 April	16 May	23 June	27 July	27 Aug.
Spiders	43.6 mg.	44.5 mg.	11.8 mg.	5.7 mg.	79.2 mg.	73.6 mg.	76.9 mg.	78.3 mg.	58.9 mg.
Insects	142.4 mg.	147.0 mg.	36.8 mg.	1108.5 mg.	171.0 mg.	132.2 mg.	107.0 mg.	78.0 mg.	43.3 mg.
Heteroptera	41.4 mg. 44.7%	85.5 mg. 58.1%	22.0 mg. 59.7%	1034 mg.** 93.2%	108.6 mg. 63.5%	35.3 mg. 26.6%	13.2 mg. 12.3%	17.1 mg. 22.0%	27.5 mg. 63.5%
Coleoptera	24.1 mg. 25.8%	39.6 mg. 26.9%	3.8 mg. 10.3%	3.3 mg. 0.3%	11.8 mg. 6.9%	8.9 mg. 6.7%	85.9 mg. 80.8%	47.6 mg. 61.0%	9.5 mg. 21.9%
Lepidoptera	16.6 mg. 17.9%	6.3 mg. 4.3%	8.5 mg. 23.2%	68.0 mg. 6.1%	45.1 mg. 26.4%	52.8 mg. 39.8%	1.7 mg. 1.5%	0.0	0.4 mg. 1.0%
Diptera	++	11.7 mg. 7.9%	1.1 mg. 3.0%	3.0 mg. 0.3%	2.6 mg. 1.5%	0.0	0.0	0.6 mg. 0.8%	1.3 mg. 3.0%
Hymenoptera	++	2.1 mg. 1.4%	1.4 mg. 3.8%	0.8 mg. 0.1%	2.9 mg. 1.7%	4.8 mg. 3.6%	2.4 mg. 2.2%	5.0 mg. 6.4%	4.5 mg. 10.5%
Orthoptera	3.4 mg.* 3.6%	0.0	0.0	0.0	*	33.0 mg. 24.8%	3.8 mg.* 3.6%	7.7 mg.* 9.9%	* 0.0
Neuroptera	0.0	1.8 mg. 1.2%	++	0.0	0.0	0.0	0.0	0.0	0.0
Others	7.4 mg. 8.2%	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

++ present, but not weighed separately, included under "Others"

\* excluding biomass of individuals too large to serve as food for spiders: 18 Sept. 49.4 mg. excluded, 2 April 65 mg., 23 June 13.8 mg., 27 July 41.1 mg., 27 Aug. 62.8 mg.

\*\* Chermids were 1011 mg., 91.1%.



**FOOD SUPPLY. QUALITY.** The arthropod biomass taken in creosote bush sweeps is itemized according to order in Table 3. Speculation on the relationships of the dominant spiders to this food supply is very tenuous since there is no information on their specific food habits. Bilsing (1920) and Bristowe (1941) give general information on the feeding of spiders, and their conclusions are the basis for most of the following speculations.

The insect biomass attained its highest level in February when spiders were almost completely absent from creosote bush; this peak was almost completely due to the flourishing of chermids, which were almost completely absent from creosote bush except in December, February and April (70, 1174 and 170 individuals/M.<sup>2</sup> respectively) though present in other shrubs. Tarbush seemed to be the preferred food plant of the chermids; they were most consistently present in numbers on this shrub, reaching peaks of 1054/M.<sup>2</sup> in February, 6160 in April and 925 in September. The chermid density for tarbush was roughly reciprocal to spider density. This reciprocal relationship may be partly due to predator pressure of the spiders on the chermids.

Homoptera, which are generally acceptable to spiders, and hemiptera, which are usually rejected, make up the bulk of the insect biomass in 2/3 of the samples. Chermids are probably a very suitable food for all spiders, of all instars, because of their small size and light chitinization. Diptera, which in general are taken by spiders in larger numbers than any other order of insects, were never present in large amounts (0-7.9 per cent of insect biomass). Small flies were the most abundant forms, and are probably an important food for *Dictyna* and small *Misumenops*. The lepidoptera biomass was almost entirely composed of larvae, which are generally not as acceptable to spiders as the adults. Coleoptera, which were most abundant in two months, generally do not form a large part of the diet of spiders, because of the size, aggressiveness, heavy chitinization and distastefulness of many beetles. The last characteristic is particularly true of Coccinellidae, which were one of the most abundant families in the present collections. Bristowe (1941) found that coccinellid larvae were refused by captive spiders. Hymenoptera were never present in significant amounts; they are generally distasteful to spiders, though ants are less so to crab spiders. This order includes potential predators of spiders, particularly crab spiders.

Auten (1925) found four species of hymenoptera and two species of diptera as parasites in the egg sacs of *Philodromus canadensis*, and one species each of neuroptera larva and reduviid adult as possible predators. *Misumenops dubius* has been found extensively in the brood chambers of mud daubers in southern Texas (Gertsch 1939).

There is possibly some cannibalism among the species of spiders in the present collections. Bilsing (1920) observed *Phidippus adax* to feed on *Philodromus* and *Xysticus*. Bristowe (1941) found, however that *Thomisus onustus* and *Misumena calycina* refused spiders offered to them, possibly because they are adapted to ambushing flying insects that come to flowers and do not recognize a crawling arthropod. The same may be true of species of *Misumenops*.

#### INTERSPECIFIC ISOLATION

A most interesting aspect of the present study is the means of coexistence of different spiders, particularly two of the same genus, in the same area. Since spiders are carnivores with presumably fairly generalized food habits, one can expect considerable competition between even distantly related species. Tretzel (1955) treats extensively the topic of intrageneric isolation and interspecific competition among spiders. The present data are in agreement with his major conclusion that closely related species "live apart in space and time" but that complete isolation is necessary only in specific situations. Interspecific competition among spiders in the area studied is reduced in several fashions: (1) vertical separation of the shrub dwelling species from ground dwelling species; (2) horizontal separation of the shrub dwelling species by their occurrence on different kinds of shrubs; (3) general differences in the type of food, largely a result of differences in behavior in capturing food; (4) seasonal differences in the time of reproduction and time of maximum abundance.

VERTICAL STRATIFICATION. *Misumenops*, *Philodromus*, *Tmarus* and most of the other genera in the present collections, as far as can be judged from the literature, are typically plant dwelling spiders, and hence do not come into competition with the ground dwelling forms. The extent to which the different jumping spiders in the collections range onto the ground is not known. The irregularity of the size frequency distribution of *Phidippus* in



the different shrub collections suggests that this species may inhabit both the ground and shrub strata, the latter possibly being of secondary importance. The completeness of the developmental record of *Sassacus papenhoei* in shrub sweeps (figure 7C) suggests that it is primarily a shrub dwelling species.

Vertical stratification of spiders has been described in forest communities. Such stratification has been attributed to temperature differences, which are particularly distinct between the soil stratum and overlying vegetation. This ground to shrub difference would be extreme in desert communities. Elliott (1930) found no difference between the spiders of the herb and shrub strata of deciduous forests and proposed that physical conditions were not sufficiently different to cause stratification. Weese (1924) emphasized the "narrowly limited" stratification of web-spinners, in which temperature and humidity are less important factors than suitable substratum. However, Lowrie (1942) concluded that humidity is probably more limiting than special substratum for web-spinners. Kuenzler (1958) found vertical stratification between three species of *Lycosa*. Tretzel (1955) considers that vertical stratification is secondary to horizontal separation, and he is almost alone in emphasizing the importance of biotic factors in such separations.

**HORIZONTAL SEPARATION.** The basis for the clearly demonstrated plant preferences—*Misumenops* spp. for creosote bush, *Philodromus* for mariola, and *Tmarus* for tarbush, probably lies in the advantage of the concealing coloration gained in these combinations. *Philodromus infuscatus* has the same light gray color as the leaves of mariola; the brown and gray mottled *Tmarus* matches the stems of tarbush better than the other shrubs; *Misumenops* show a range of colors, particularly of the large abdomen—brown, yellow-brown, yellow, yellow-green, green, reddish, allowing them to blend with the live, green leaves of creosote bush, with its yellow flowers, or with the yellows and browns of dying leaves. *Tmarus angulatus* is also concealed by its body shape, the posterior-dorsal projection of the abdomen; at rest it clasps a twig with its legs, and by its form resembles a bud or petiole stump (Comstock and Gertsch 1940).

The concealing coloration of these genera has been frequently noted in the literature. For example: *Philodromus virescens* has the same bluish-gray color as sagebrush, on which it is com-

monly found (Gertsch 1939). *P. alascensis* has a gray coloration like the sand of the foredunes where it occurs (Lowrie 1942). The red markings of *Misumenops asperatus* allow it sometimes to resemble exactly the flowers of *Rhus acetosella* on which it occurs (Lovell 1915).

The ability of Misumeninae to change color also has been often remarked. Pearse (1911) found that 84 per cent of the white individuals of *Misumenoides aleatorius* and *Misumena vatia* were collected from white flowers, while 85 per cent of yellow individuals were from yellow flowers. Gertsch (1939) found that *Misumenops asperatus* is able to reversibly change its color. Gabritschevsky (1927) studied this response in various instars of *Misumena vatia*. He found that the white coloration is due to permanent deposits of guanin pigment, and a pink pigment also develops and accumulates with age. Yellow pigment, which masks the white, is temporary and develops in response to reflected yellow light. Only mature spiders can form this yellow pigment. The change from white → yellow can be accomplished in 1 to 10–20 days, and a return to white in 5–6 days.

Specific plant preferences have been noted for a few other spiders. Fautin (1946) found *Sassacus papenhoei* in the shrubs of the greasewood fasciation of sagebrush desert, but not in other communities. Dowdy (1950) found *Dictyna volucripes* abundantly in *Lespedeza*, but rarely in *Scirpus*—*Echinochloa* only 45 yards away. There may also be a response to a habitat type rather than plant species. Blake (1926) concluded that the simple presence of a forest cover was a major factor in the occurrence of forest spiders. Of the 48 species classified as true forest spiders in beech-maple forest, 46 also occurred in oak-hickory and 40 in elm-maple (Elliott 1930).

ISOLATION BY FOOD AND FEEDING HABITS. By their mode of life and their hunting methods, different spiders tend to contact particular kinds of insects and become adapted within wide limits to capturing and feeding on these kinds (Bilasing 1920, Bristowe 1941). This seems to be the case for the crab and jumping spiders of the present study.

No specific observations have been published on *Misumenops*, but species of this genus are stated to all be semisedentary and ambushers of their prey, as are *Misumena* and *Misumenoides* (Gertsch 1939). Therefore, these spiders probably are dependent



on insects that are attracted to flowers, such as various flies and bees; beetles coming to flowers may be fairly immune to capture. Crab spiders more often attack and successfully capture prey larger than themselves than do jumping spiders. *Misumena vatia* sometimes makes no attempt to go after its prey, but waits until an insect flies or walks into range of its elongate front legs. As observed by Thomas (1952) the behavior of *Misumena vatia* and several other ambushing crab spiders is adjusted to the kind of prey, as if the spider were instinctively informed of the means of defense of each kind of insect. These spiders were observed to circle a bee until they had an opportunity to bite into the back of the neck and quickly paralyze the large prey. If this approach could not be made, the spider abstained from attacking. Other approaches occurred only accidentally when the prey moved suddenly. Flies and other unarmed insects were grasped ventrally or in any chance position, and were not necessarily paralyzed by a neck bite before feeding began. Bristowe (1941) found that *Misumena* and *Thomisus* may ignore crawling insects, possibly because they are instinctively accustomed to flying forms.

*Tmarus* and *Philodromus* also probably largely depend upon lying in wait for their prey, taking advantage of their concealing coloration, but they frequently change their position, and thus presumably encounter and capture insects that are not concentrated by the attraction of flowers, such as the different homoptera and hemiptera that are sucking juices on various parts of plants.

Many jumping spiders, and presumably *Sassacus papenhoei*, actively search for and pursue their prey. Because of their supposed superior sight, and their extreme mobility, they may not need the additional advantage of concealing coloration. The abundant jumping spiders in the present study showed no plant preferences. Bilsing (1920) found *Phidippus* feeding principally on hemiptera, hymenoptera, orthoptera and diptera. No beetles were observed to be taken. Insects' immunity from attack from these active hunting spiders depends on larger size, chitinization, disagreeable odor or taste, and/or warning movements.

*Dictyna* are able to capture only very small insects, as flies, which they can trap in their small webs. Argiopidae, such as the *Metepeira labyrinthica* observed by Bilsing (1920) probably have

the most diverse diets, i. e. anything palatable that blunders into their extensive webs.

**PEAK OF REPRODUCTION AND ABUNDANCE.** Most of the spider populations in the present study area had different times of maximum abundance (figure 3), except that most of them are overlapped by *Misumenops*, and there is also a certain separation of the times of reproduction, as estimated from the abundance of mature individuals. Similar temporal separation of peaks of abundance is seen in the graphs of Weese (1924), and the importance of temporal isolation of times of reproduction is stressed by Tretzel (1955). Since a spider population's food requirements are greatest during its peak of abundance, and at the time of reproduction, any separation in time of these periods for different species is advantageous in reducing competition and allowing a more diversified group of species to fit together in a community.

*Misumenops dubius* versus *M. coloradensis*. These two species have their peaks of reproduction at the same time and have the same plant preference. Judging from the numbers of mature individuals, *dubius* was somewhat more abundant. The copulatory organs of the two species are quite distinct, and this is probably the major barrier to their interbreeding. The period of abundance of mature *coloradensis* is seasonally more limited than that of *dubius*, and this is probably of secondary importance in reproductive isolation of the species.

With the continuing faith in the "principle of competitive exclusion", or "one species to a niche" (Hardin 1960), it may be assumed that there is some ecological difference yet to be discovered between these two very closely related species that allows them to coexist successfully. There are other instances of coexistence of species of the same genus. Kuenzler (1958) in a study of three species of *Lycosa*, could find no apparent factors separating two of them; the smallness of their home ranges and certain differences in the way they wander over this area may be important. Tretzel (1955) in an intensive study of 365 species in the vicinity of Erlangen, Germany, found four pairs of species coexisting, the members of each pair having apparently identical ecological requirements and similar times of reproduction. However, all of these situations showed characteristics that may explain their coexistence. (1) All pairs lived in habitats with a greater than average food supply, and showed considerable movement between strata. Both of these conditions would reduce the



importance of competition for food as can possibly be interpreted for other situations reported in the literature, for example Ross (1957) for coexistence of sycamore leafhoppers. If there is a surplus food supply for two species having the same food requirements, and if other factors are operative to prevent their increase to the point of full utilization of their food supply, they may then coexist without competition. This can particularly be pictured as happening in a habitat having physical conditions considerably suboptimal for both species. (2) In three of the four pairs, one species showed a peripheral abundance around a center of distribution where it was less abundant, while the other species was centrally abundant. This possibly represents a situation where a horizontal ecological separation is developing. One species with greater range of tolerance is moving out into a peripheral region, initially less suitable, and gradually disappearing from the central region where the other species has a slight competitive advantage. That is, this is a situation where elimination of one of two species from the same niche is slowly in progress. It is not known whether either of these situations exists with regard to *M. dubius* and *M. coloradensis*, but their example supports Tretzel's conclusion that "the necessity for intrageneric isolation is compelling only under entirely specific conditions".

#### SUMMARY AND CONCLUSIONS

1. The spiders of a southern desert shrub community were studied by analysis of 48-sweep collections from the dominant (*Larrea divaricata*) and subdominant shrubs (*Flourensia cernua* and *Parthenium incanum*).

2. The spider fauna of 20 species was dominated by *Misumenops dubius* and *M. coloradensis*, with *Philodromus infuscatulus*, another crab spider, and *Sassacus papenhoei*, a jumping spider, as numerical subdominants. Only these four species exceeded 5 per cent of the total number of individuals; 11 species exceeded 1 per cent.

3. Spider abundance ranged from 2800 to 36,000 per hectare, and biomass ranged from 11 to 150 grams per hectare. The number of spiders in the shrubs reached a minimum in February, when winter temperatures were lowest. A fairly constant density, more than 50 per cent *Misumenops*, of 34,000 to 36,000 per hectare was maintained from April through August.



Individual species showed peak densities before or after the June period of maximum temperature and minimum humidity. *Misumenops*, which were abundant from April through September, showed a depression of numbers in June. *Tmarus angulatus* was unusual in showing its highest numbers in June and December.

4. Densities per unit of vegetation ranged from 2.0 to 25.0/M<sup>2</sup>, and biomass from 2.5 to 104.7 mg./M<sup>2</sup>. There was some variation of density attributable to the degree of development of leaves and flowers of the different shrubs.

5. Three species of spiders showed definite shrub preferences, *Misumenops* spp. for *Larrea*, *P. infuscatus* for *Parthenium* and *T. angulatus* for *Flourensia*.

6. *Misumenops* spp. reproduce throughout much of the year, but principally in July and August. They move completely out of the shrub stratum in winter, overwintering as juveniles of different instars, and then quickly return to abundance in *Larrea* with moderation of winter temperatures in April. Male *Misumenops* reach maturity in about the 6th instar and females in the 8th.

7. *Philodromus infuscatus* reproduce only in September and October; after a long period of absence from the shrub stratum, possibly overwintering in the egg sac, individuals develop synchronously to maturity.

8. *Sassacus papenhoei* also has only one generation per year, born in July and August, and developing uniformly. This species remains active in the shrubs in winter.

9. Biomass ratios of spiders (predators): insects (prey) averaged 13.3–47.2 per cent for the different shrubs. The insects must have a much greater rate of production to be able to serve as the food base for the spiders.

10. Spider densities in this southern desert shrub vegetation are considerably higher than those reported for northern desert shrub (sagebrush) but less than the densities reported for more densely vegetated communities.

11. The predominance of crab spiders and jumping spiders (hunting forms) over web-spinners (ratio of 50 : 3 individuals) is probably due to the sparseness of the vegetation, which provides few sites for webs and leaves orb weavers exposed to predators, and to high air movement, destructive to webs.

12. The temperature and evaporative stress of this desert area do not exceed the limits of tolerance of many spiders, but these factors are undoubtedly important in selecting those species than can best survive. The literature shows that there are considerable differences in the preferences, temperature of heat paralysis and critical temperature for water loss of different spiders.

13. The coexistence of the two species of *Misumenops*, having the same time of reproduction and same plant preferences, and presumably similar food habits, cannot be explained with the present data.

14. Competition between *Misumenops* spp., *P. infuscatus*, *T. angulatus* and *S. papenhoei* is reduced by their partial horizontal separation onto different kinds of shrubs, general differences in food habits, and temporal separation of periods of peak abundance of numbers and of reproduction.

The basis for the plant preferences is probably the concealing coloration gained on the preferred plant.

*Misumenops* are semisedentary ambushing spiders and probably depend largely on diptera and hymenoptera attracted to flowers. *Philodromus* and *Tmarus* probably depend on ambushing tactics to capture food, but move about and thus presumably contact and depend upon the various heteroptera for food. *Sassacus* probably actively seeks and pursues its prey.

15. Though the spider fauna of this desert shrub vegetation is not very diverse, it is developed to exploit rather fully the limited resources of the desert habitat.

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